

Diversity of fruit-feeding butterflies (Nymphalidae) along a gradient of tropical rainforest succession in Borneo with some remarks on the problem of “pseudoreplicates”

Jan BECK¹⁾ and Christian H. SCHULZE²⁾

¹⁾ Department of Animal Ecology and Tropical Biology (Zoology III), Theodor-Boveri-Institute for Biosciences (Biozentrum), Am Hubland, D-97074 Würzburg, Germany

²⁾ Department of Animal Ecology I, University of Bayreuth, D-95440 Bayreuth, Germany

Abstract Species richness and diversity of fruit-feeding butterflies in six different forest types in Kinabalu National Park, Sabah (Borneo) were compared. The six sampling sites were situated in a primary rainforest, another old-grown forest of unknown history, three successional forests after commercial logging activities (approx. 30, 15, and 5 years ago), and a farmland site next to a local village. Butterflies were caught alive in traps using rotten bananas as bait. Species diversity was measured by Fisher's α of the logarithmic series. Species total was estimated by the “MMMeans”-method (Colwell, 1997). The primary forest contained most species and the highest diversity, on the farmland site the lowest number of species was found. The secondary forest sites were intermediates between the former two habitats with regard to their diversity and species richness, with the 15 year old site showing a more diverse fauna than the 30 or 5 year old site. Although almost none of the differences in diversity can be considered statistically significant (presumably due to low sample sizes), the results show patterns of diversity that correspond well with data for other Lepidoptera taxa (Geometridae, Pyralidae) from the same sites. If pseudoreplicates had not been recognized by individual marking of the butterflies, confidence limits for α -values would have been underestimated, and α -values themselves overestimated in most cases. The degree of deviation from true values differs between the habitats. For two fruit-feeding nymphalid butterflies, we reported maximum life spans of 45 (*Neorina lowii*), respectively 41 days (*Basseronia dunya*).

Key words Nymphalidae, biodiversity, habitat gradient, Borneo.

Introduction

Degradation of tropical forest habitats is a major issue in conservation biology concerned with the protection of species diversity. It is assumed that the majority of terrestrial animals can be found in tropical rainforests (Wilson, 1992). Despite this, the destruction of these habitats goes on at great speed (*e. g.* Bowles *et al.*, 1998; Laurance, 1998; Meyers, 1992), converting primary rainforests into different types of secondary landscapes ranging from eroded wastelands through agricultural and plantation areas to naturally developing successional forests. The impact of this landscape conversion on species diversity is still poorly understood, given the huge variety of taxonomic groups with possibly differing reactions to human-caused disturbance (*e. g.* Chung & Mohamed, 1996; Dahaban *et al.*, 1996; Eggleton *et al.*, 1997; Intachat *et al.*, 1997).

In searching for quick-acting conservation strategies which are enforced by the speed of destruction of primary forests, secondary forests may play a major part in preserving at least a part of tropical biodiversity (Lugo, 1992) of which, in terrestrial habitats, insects are a taxon of dominant importance (Hammond, 1992; Stork, 1988). Detailed data would be necessary to assess how much of this diversity can be protected in secondary landscapes. Extinction of

species due to landscape conversion may be divided up into two effects: immediate extinction because of habitat loss, or delayed extinction because of thinning of population sizes by habitat fragmentation or degradation (*e. g.* Newmark, 1991). The latter effect is particularly difficult to appraise and hard to distinguish from naturally occurring events of local extinction. However, despite these theoretical problems it is worth using field data on species diversity in disturbed habitats adjacent to protected areas as a first step in assessing the impact of disturbance on local extinction processes.

In this paper we present some data on the change of diversity, species richness and abundance of the guild of fruit-feeding butterflies along a human-caused successional gradient of tropical rainforest in Sabah, Borneo. Additionally, we analyze the influence of pseudoreplicates on bait trapping results.

Methods

Field methods

The field work for this study was conducted from October to December 1997 in the vicinity of the village Serinsim at Kinabalu National Park, Sabah (Malaysia) (Fig. 1). Kinabalu Park in the North-East of Borneo contains a large area of primary rainforest in a rugged mountain terrain, while around the park the landscape is mostly clearcut and converted into farmland or plantations (*e. g.* softwood and palm oil). A closer description of Kinabalu National Park can be found elsewhere (*e. g.* Häuser *et al.*, 1997; Kitayama, 1992; Wong & Phillippo, 1996). The village of Serinsim (= Sorinsim) is situated at the northern border of the park in a hilly lowland region (6°18'N, 116°42'E; Häuser *et al.*, 1997). Some forested areas in this region have been logged and included in the park afterwards, thereby producing sites of successional secondary forest adjacent to primary forest. Within a 10 km radius six sites were selected for comparison with regard to diversity, species richness and abundance of fruit-feeding butterflies: An area of primary dipterocarp rainforest (PDF, 430 m a.s.l.) (Fig. 4), an old, highgrown forest close to a riverbed with an unknown history of possible human disturbance (OF, 270 m a.s.l.), three sites of secondary forests with the approximate ages 30, 15 and 5 years (SF30, 180 m a.s.l.; SF15, 275 m a.s.l.; SF5, 180 m a.s.l.), and a farmland-site close to the village (cultivation of *Oriza* and *Zea*; FAL, 170 m a.s.l.) (Fig. 3), surrounded by secondary bush vegetation typical of degraded, clearcut fallow land areas in Sabah.

The butterflies were caught alive in traps baited with rotten bananas (trap design: *e. g.* Schulze, 1996; Sourakov & Emmel, 1995). The traps were controlled every day while active, the bait being replaced when it was dried out or lost (presumably due to squirrels). For identification of caught specimens, taxonomy and nomenclature, we follow standard reference works for the region (Corbet & Pendlebury, 1992; Otsuka, 1988). Only specimens of difficult taxa (*e. g.* *Chersonesia* spp.) were killed for identification, released specimens were marked with numbers to recognize recaptured individuals (see Fig. 2).

Assessment of species diversity and species richness

We define species richness here as the number of species of a taxonomic group that can be found in a habitat in a given time-span. Therefore it is expressed as an absolute number of species. Species diversity on the other hand is a rather diffuse concept (Taylor, 1978; Hurlbert, 1971) that somehow relates species richness to the number of individuals present in the habitat. Diversity is measured in abstract diversity-indices or species-accumulation functions (*e. g.* Taylor, 1978). The exact definition of "diversity" is then dependent on the

chosen kind of measurement and its mathematical basis. When comparing different habitats, species richness and diversity would probably produce similar results in most practical situations.

Fisher's α from the logarithmic series (Fisher *et al.*, 1943) was used as a measure of species diversity independent of sample size because of its manifold advantages discussed elsewhere (Taylor, 1978; Robinson, 1998; Southwood, 1978; May, 1975). Given confidence limits show the range in which 95% of the α -values would be expected to fall if another sample from the same butterfly community was collected. The 95% confidence intervals were calculated using the formula $[1.96 \sqrt{\text{var } \alpha}]$, based on α 's variance according to Anscombe (1950). Computations of α -values and variances were done with the computer program "divers" (Krebs, 1989). Some authors (*e. g.* Robinson, 1998) prefer the original variance given by Fisher *et al.* (1943), which, in our set of data, enlarges confidence limits slightly.

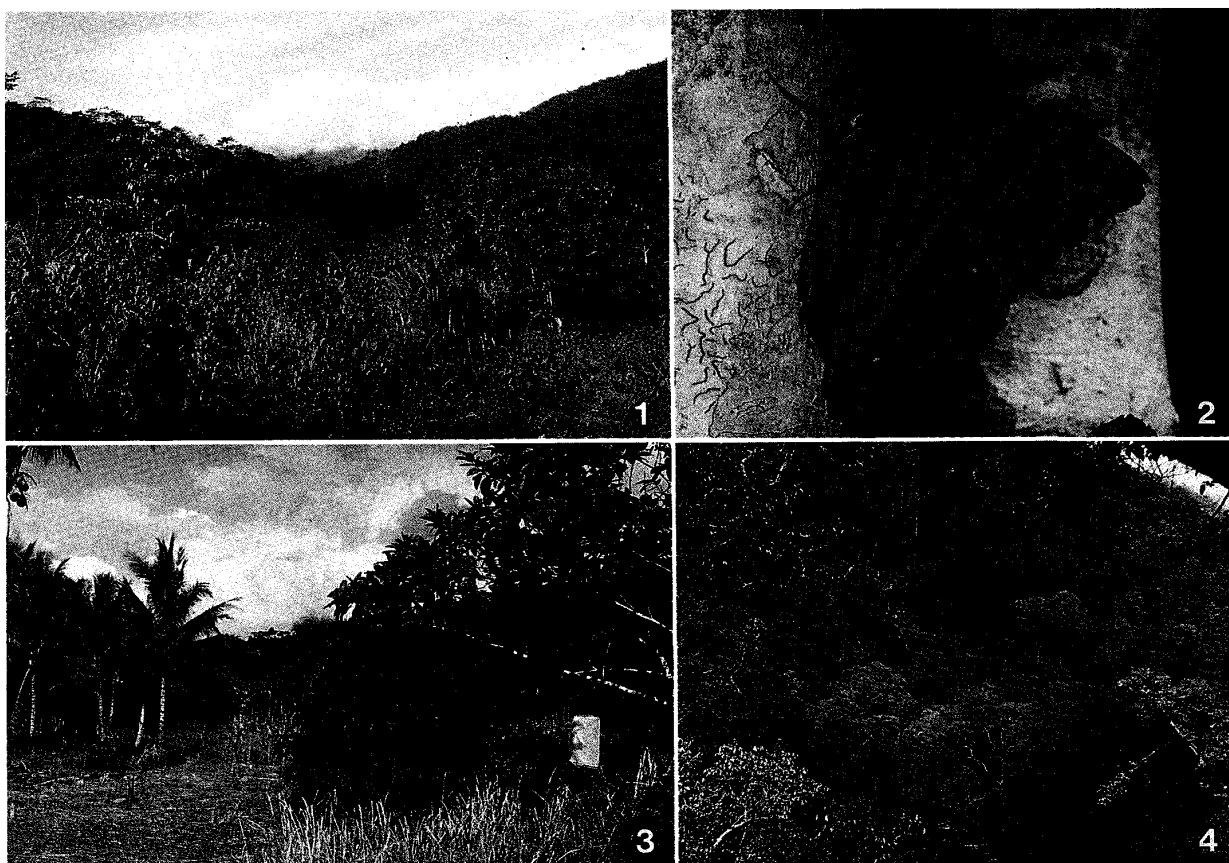
To compare species richness at different sites, it makes little sense to use the actually collected numbers of species, since they can be expected to depend strongly on sample size (number of individuals), if the species of a community are not completely recorded (*e. g.* Taylor, 1978; Southwood, 1978)—a case hardly ever reached when dealing with tropical invertebrates. Colwell and Coddington (1994) described several sophisticated methods to estimate true species richness of a habitat from non-complete data as it is typically found in field studies. We present here estimates for true species number calculated by the "MMMeans"-method; computations of these estimates were done with the computer program "EstimateS" (Colwell, 1997; see also Colwell & Coddington, 1994 for a closer description). We preferred this method over others because of its logic and because it produced reasonable estimates in different sets of data already tested (Beck, 1998; León-Cortés *et al.*, 1998; Schulze *et al.*, in press; Süsenbach & Fiedler, 1999).

The computer program mentioned above also calculates estimates for species richness as well as for Fisher's α , if sample days in the averaged species accumulation curve (after randomization of sample order) are left out, thereby giving the opportunity to check if the data base is sufficient to produce stable estimates and indicators of diversity or if it is so scant that they are still dependent on sample size.

Table 1. Sample effort, results, and the calculated estimates of species richness for the six habitat types are given, considering data both excluding, respectively including pseudoreplicates caused by recaptures of individuals. The last two columns show estimates of "true" species richness of the different habitats, as computed by the "MMMeans"-method (Colwell 1997).

Site	Trap-days	Individuals		Species		Estimated number of species	
		without recaptures	with recaptures	without recaptures	with recaptures	without recaptures	with recaptures
PDF	17	30	36	16	16	41	31
OF	30	66	95	17	17	22	20
SF30	34	25	29	10	11	17	18
SF15	17	15	18	9	10	27	32
SF5	36	39	60	9	10	10	10
FAL	22	57	—*	8	—*	9	—*

* no recaptures



Figs 1-4. Habitats and a marked *Amathusia* specimen. 1. Vicinity of village Serinsim (Mount Kinabalu National Park). While the village is surrounded by secondary bush vegetation (in front), the adjacent hills are covered with forests of different age. 2. A marked male of *Amathusia phidippus* which was caught by bait trap and released afterwards. 3. Farmland site (FAL) close to village Serinsim with installed bait trap. 4. Primary dipterocarp forest (PDF) where trapping was conducted.

The identical diversity calculation procedures were performed on the data including recaptures of marked specimens to study the influence of pseudoreplicates on diversity measurements.

Results

A total of 232 nymphalid butterflies, belonging to 28 species, was caught in the traps. Adding the recaptured individuals, 296 butterflies have been caught, which is an increase of 21.6%. When considering the rather large effort of 156 trap-days (distributed unevenly over the six sites for logistic reasons), the number of collected individuals seems quite low. Table 1 shows the number of trap-days, individuals, species and the estimated "true" species richness (as calculated by the "MMMeans"-method) for the six habitat types. Species richness, measured by the estimated number of species, was by far greatest in the primary forest (PDF), lowest at the farmland site (FAL), and intermediate in the other forest types. In the old riverside forest (OF) and in the 15-year-old secondary forest (SF15) it is higher than in the 30-year-old (SF30) and the 5-year-old secondary (SF5) forests (Table 1). Most estimates seem reliable in the sense that they did not change by more than 5% of their value if three or less average sample days are subtracted from the computation process. However, at the

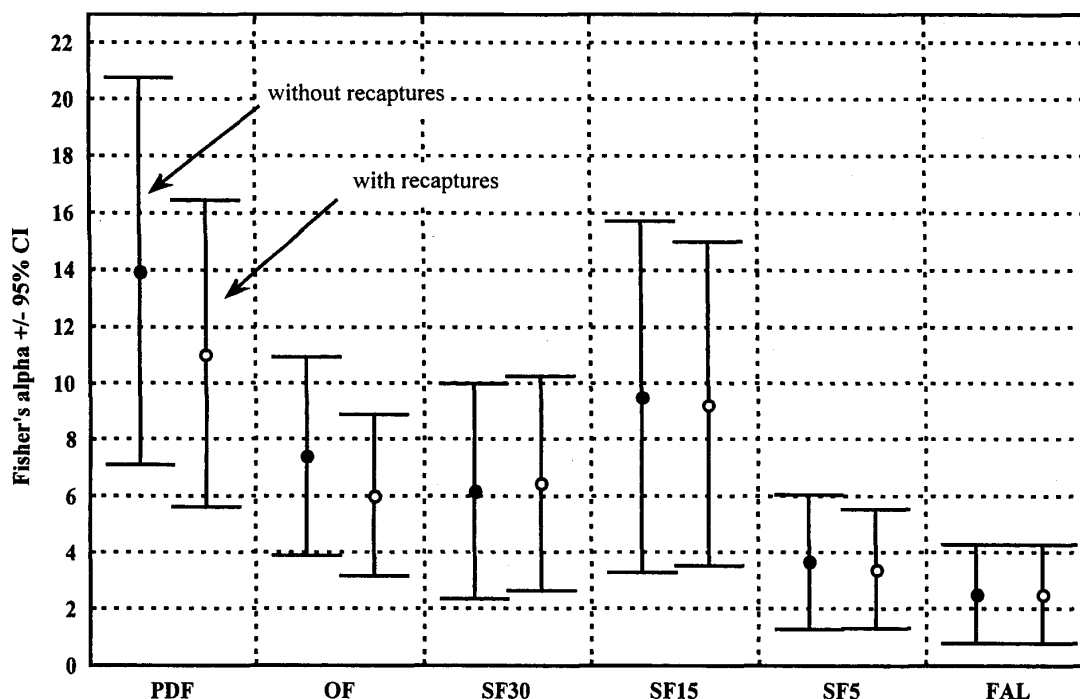


Fig. 5. Fisher's α values for the guild of fruit-feeding butterflies at six landscape types in Kinabalu Park are shown. The primary forest (PDF) has higher values than any other site, the other forest types obtain intermediate values with a surprising high diversity at the 15-year-old secondary forest site (SF15), while the farmland site (FAL) shows the lowest α -values. Confidence limits are large, leaving only the differences between the primary forest and the farmland as well as the 5-year-old secondary forest (SF5) statistically significant. The confidence limits are based on α 's variances according to Anscombe (1950).

PDF and the FAL this change was greater than 5%, and both estimates still seem to be in an upward trend with increasing sample size (data not shown).

Fisher's α values show very similar trends as the expected number of species in Table 1, showing the highest diversity in the PDF, the lowest in the FAL, and an unexpected high value in the SF15 (see Fig. 5). As can be seen by the overlap of the confidence bands, almost none of the differences in diversity described here is statistically significant at a 5% error probability, which is not surprising when considering the low sample sizes (Table 1).

Including the recaptures in the analysis, the Fisher's α -values decrease for most sites with recaptures. Additionally the span of the 95% confidence intervals changed. However, the change of α -values and confidence intervals varies between sites due to different recapture rates. In one habitat (SF30) the α -value calculated by data including recaptures surpasses the one without recaptures, because individuals already marked in the neighboring habitat were found here, thereby increasing the species number in that habitat. Due to relatively low recapture-rates at most sites, the general diversity pattern of the habitats do not change much in this study.

Recapture rates were very different in the habitats, ranging between zero (FAL) and 54% (SF5) of the individuals caught at the sites. Most recaptured individuals were trapped only once again, but some kept on being seen, as much as twelve times in one case. In two cases individuals were seen in habitats different to those where they had been marked, as mentioned

above.

In two cases, individual life spans of at least 45 (*Neorina lowii*) and 41 days (*Bassarona dunya*), respectively, could be deduced from the recapture data.

Discussion

Species diversity

Both measurements for species richness and diversity indicate that the primary rainforest site is by far more valuable than any other site in terms of its butterfly fauna, if the two criteria mentioned above are considered significant for conservation (e. g. Reid, 1998; Schulze & Fiedler, 1999). The higher the degree of disturbance of the sites, or, more precisely, the younger the forest's successional state, the lower was its butterfly species richness and diversity. An exception is the 15-year-old site that housed an unexpectedly high number of species. Almost none of these results can be considered statistically significant, a fact most likely caused by the rather low number of individuals caught. In spite of this, it is surprising that the results presented above not only fulfill reasonable assumptions and conservationists' "common sense prejudices" for tropical areas (such as expecting the highest diversity in the

Table 2. A list of the species found in this study. The number of caught individuals (without recaptures) is given for every bait trapping site.

Species	PDF	OF	SF30	SF15	SF5	FAL	Σ
<i>Amathusia phidippus</i> (Linnaeus, 1763)		1				2	3
<i>Amathusia</i> spec. (non- <i>phid.</i>)		1					1
<i>Amathuxidia amythaon</i> (Doubleday, 1847)				1		1	2
<i>Bassarona dunya</i> (Doubleday, 1848)	3	15					18
<i>Chersonesia intermedia</i> (Martin, 1895)		1	1				2
<i>Chersonesia rahria</i> (Moore, 1858)		8			1		9
<i>Cirrochroa</i> (?) <i>tyche</i> (Felder & Felder, 1861)	1						1
<i>Coelites euptychioides</i> (Felder & Felder, 1867)	1						1
<i>Elymnias nesaea</i> (Linnaeus, 1764)						2	2
<i>Kallima limborgii</i> (Moore, 1879)	1	2					3
<i>Lexias dirtea</i> (Fabricius, 1793)	1	1	1				3
<i>Lexias pardalis</i> (Moore, 1878)	1	1					2
<i>Melanitis leda</i> (Linnaeus, 1758)				2	1	29	32
<i>Mycalesis anapita</i> (Moore, 1858)			1	4	8	6	19
<i>Mycalesis horsfieldi</i> (Moore, 1892)					1	15	16
<i>Mycalesis kina</i> (Staudinger, 1892)	1	6	1				8
<i>Mycalesis maianeas</i> (Hewitson, 1864)	4	3					7
<i>Mycalesis orseis</i> (Hewitson, 1864)	1	1	2	2	16	1	23
<i>Neorina lowii</i> (Doubleday, 1849)	4	16	5		5		30
<i>Orsotriaena medus</i> (Fabricius, 1775)						1	1
<i>Prothoe franck</i> (Godart, 1824)	1		2	1	2		6
<i>Ragadia makuta</i> (Horsfield, 1829)	2	3	9		4		18
<i>Stibochiona schoenbergeri</i> (Honrath, 1889)		1					1
<i>Xanthotaenia busiris</i> (Westwood, 1858)				1			1
<i>Zeuxidia amethystus</i> (Butler, 1865)	5	1	1	2			9
<i>Zeuxidia aurelius</i> (Cramer, 1777)	1	3	2	1			7
<i>Zeuxidia doubledayi</i> (Westwood, 1851)	2	2		1	1		6
Spec. ? (Satyrinae)	1						1

primary rainforests, the lowest at the farmland site), but also correlate well (as far as we know by now) with much larger data-sets for other Lepidoptera that we caught at the same sites. Geometrid moths collected at UV-light show a very similar pattern of diversity (Beck, 1998), including an even more pronounced peak at the 15 year old site.

In this study, we refrained from an analysis of β -diversity between the six habitats, although the data (see Table 2) suggest that rather strong separations in the species composition between young and old habitats might be found. The use of similarity indices is not considered reliable with sample sizes as low as ours (*e. g.* Wolda, 1981) for several reasons, including the fact that incidence-based similarity indices produce a (downward) bias with non-complete samples of a species rich community (*e. g.* Lande, 1996).

The likelihood that differences in species composition are only the result of increasing altitude along the studied gradient ranging from 170 m (FAL) to 430 m (PDF) is rather low. Even the recorded butterfly fauna of a hill forest at Poring (southeastern border of Mount Kinabalu National Park) situated at higher altitude (450–800 m) is still very similar to the lowland butterfly fauna at Serinsim (compare Häuser *et al.*, 1997).

Pseudoreplicates and longevity

The recognition of diversity patterns along the gradient of disturbance would be—in the case of this study—similar when adding the recaptures to the data, but if recapture rates were higher even a changed order of habitats (with reference to their diversity) might result from pseudoreplicates because recapture rates were different between the habitats. Theoretically, differences in diversity between sites might be considered statistically significant only due to the increase of sample sizes by pseudoreplicates. Therefore we suggest that only studies that largely eliminate the possibility of pseudoreplicates should be considered reliable with regard to an evaluation of a habitat's biodiversity.

Especially in fruit-feeding Nymphalidae, a strong impact of pseudoreplicates should be expected because of the longevity of some species. Our data support that at least some species may live up to six weeks in the field. Life spans of up to six months in some neotropical, pollen-feeding *Heliconius* species (Heliconiinae) can be achieved only due to their unusual adult diet rich in amino acids (*e. g.* Dunlap-Pianka *et al.*, 1977), while the manifold adult diapause states in non-tropical Nymphalidae make a comparison of life spans impossible. So far no data on the life span of Southeast Asian fruit-feeding nymphalids exist.

Primary forest versus disturbed habitats

When comparing the results presented above to other studies, the picture is ambivalent: For some herbivorous groups in tropical landscapes it was shown that the species diversity of primary rainforests is unmatched by any landscape with a significant degree of human influence (*e. g.* Noctuidae, Geometridae and other night-flying Lepidoptera: Holloway *et al.*, 1992; Barlow & Woiwod, 1993), and that heavily disturbed, open sites usually have a diversity lower than any forest types (*e. g.* Mathew & Rhamathulla, 1995; Intachat *et al.*, 1997). On the other hand, for some taxa this effect is not very strong or even opposite (*e. g.* butterflies: Kremen, 1994, Spingidae: Schulze, own observation).

A main problem of a large proportion of studies like this is the fact that the studied disturbed areas were not far away from pristine primary forest sites. The latter could act as sources for

colonization of neighboring secondary forest sites.

It has to be kept in mind, that only for a few of an incredibly large number of arthropod groups any such data has been systematically collected. Therefore, we are far from watching a complete picture of diversity's reaction to human disturbance and landscape conversion. Lepidoptera have often been used as "indicators" of diversity (*e. g.* Daily & Ehrlich, 1995; Kremen, 1994), but in just a few cases (*e. g.* Schulze & Fiedler, 1998; Beccaloni & Gaston, 1995; Murphy & Wilcox, 1986) the general "indicator-concept" has been tested on a local or regional scale by correlations of the diversity of different taxa. When considering the great differences in resource needs an organism can possibly have, a clear answer to the questions of where overall diversity is highest, and why, can therefore not (yet) be expected—as is the case with many tasks in community ecology.

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摘 要

ボルネオの熱帯雨林の遷移段階と果実食性蝶類の多様性と「偽模写」の問題について (Jan Beck and Christian H. Schulze)

果実食性チョウ類の種数と種多様性を、ボルネオ島サバ州のキナバル国立公園内に見られる6つの異なるタイプの森林間で比較した。サンプリングを行った6つの調査地区は、原生林、歴史の解っていない老熟林、営利的に伐採された遷移段階の異なる3つの二次林（すなわち、伐採後各々約30年、15年、5年経過した二次林）、および村落に近いブッシュに囲まれた農地であった。各調査地区でのチョウの捕獲には、腐ったバナナを使用したベイトトラップを用い、チョウは生かしたまま捕えた。捕獲個体はマーキングした後にその場に放った。各調査地区のチョウ群集の種多様性は、Fisherの対数級数則の α を用いて算出した。また、各地区のチョウ群集の総種数は、Colwell (1997)の“MMMeans”法を使用して見積りした。

原生林地区は最大の種数と種多様性を示したのに対し、村落に近い農地は最も低い種数を示した。3つの二次林地区の種数と種多様性は、これらの地区の中間の値を示し、中でも伐採後15年を経た二次林区において、伐採後約30年、および5年経過の二次林区よりも多様なチョウ類群集が確認された。おそらくサンプル数が少ないことに起因して、調査地区間における種多様性の違いの多くは統計的に有意とはならなかったが、群集間で示された多様性の変化パターンは、同じ調査地区より得られた他の鱗翅目（シャクガ科、メイガ科）のデータの解析結果とよく一致していた。

各調査地区のサンプルにおいて再捕獲個体数を含めた解析を行うと、再捕獲の認められた多くの地区でFisherの α の値が低下した。すなわち、マーキングによるチョウの個体識別を実施し、サンプルへの再捕獲による個体数の擬似的増加の影響を除去すると、多くの場合で α 値の信頼限界が低く見積もられ、また α 値そのものは高く見積もられるだろう。 α 値およびその95%の信頼区間は、再捕獲個体数を含めたデータと含めないデータ間で変化し、その変化の大きさは、地区ごとに再捕獲率の大きさの違いに密接に関係していた。従って、サンプリングにおいて再捕獲が高率で生じるような方法や調査地の場合、偽模写の群集パラメータに対する影響が大きいために、マーキング等の実施による偽模写の影響が除去できる手法が採用されるべきである。なお、今回の個体識別調査により、タテハチョウ科の果実食性種 *Neorina lowii* (シロモンムカシヒカゲ) で45日、*Bassarona dunya* (ドゥンヤリクイナズマ) で41日の最長寿命（最長再捕間隔）が確認された。

[文責: 北原 正彦]

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